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Evolution of group size in the dolphins and porpoises: interspecific consistency of intraspecific patterns

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I investigated group size variability in dolphins and porpoises using intraspecific comparisons. Explanatory factors considered in the analysis were variables of the physical environment, the diet, and the life history of the species. Open habitat and small body size were viewed as increasing predation risk. This pattern was apparent in Risso's dolphins (*Grampus griseus*) and weakly apparent in bottlenose dolphins (*Tursiops* spp.). Group size was negatively correlated with body size in pilot whales (*Globicephala* spp.) and positively correlated with the openness of habitat in killer whales (*Orcinus orca*), striped dolphins (*Stenella coeruleoalba*), and common dolphins (*Delphinus* spp.). No such relationship was found for harbor and Dall's porpoises (*Phocoena phocoena, P. dalli*). Group size also seemed to vary depending on other physical measures of the habitat, which may indirectly reflect diet; group size showed U-shaped patterns if related to temperature. The predictive power of variables comprising detailed prey information on group size was variable. For example, pilot whales had smaller group sizes when they fed more on mesopelagic fish and less on mesopelagic cephalopods, and common dolphins had larger groups if they fed on varying types of fish. In most Delphinoidea species, group size could be described by the variables considered in this study. But each species showed its own pattern of correlations between group size and a specific set of explanatory variables. Thus, no general and consistent relation between group size and the other variables was found. It remains unknown whether these species-specific patterns result from a historical process or whether they are specialized adaptations. *Key words:* group size, Delphinoidea, diet, environment, evolution, intraspecific patterns, interspecific patterns. *[Behav Ecol 13:583–590 (2002)]*

Most comparative studies dealing with the evolution of group size compare related species. However, within-species variability of group size weakens the effects found in such interspecific comparisons (Gittleman and Decker, 1994). It is also important to consider intraspecific variation in social systems (Lott, 1984) because such flexibility demands behavioral mechanisms from which the observed variety emerges in an interaction of the behavioral mechanisms with the environment during the ontogenetic development.

If the same or similar selective forces act on different species, one would expect that these species would show similar relationships between group size and measures of behavioral ecology. This is expected especially for closely related species, though common ancestry is a confounding factor. If a series of species shows differing relationships, interpretation is more difficult. Either each species shows its own pattern because of its unique evolutionary history and its unique adaptation to the specific environment, or we are tempted into overinterpretation because the different patterns might indicate only weak influence of the ecology on group size and indicate that differences emerge due to accidental historical processes. Unfortunately, to my knowledge, there is no published study that compares intraspecific patterns over several species and addresses these issues. Most studies on the evolution of group size focus on cost and benefits of behavioral strategies in the contexts of feeding (cooperative foraging), defense of resources against conspecifics, or self-defense against predators (e.g., Lee, 1994; Rodman, 1988; van Schaik and van Hoof, 1983; Terborgh and Janson, 1986; Wrangham, 1980).

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Comparative research on dolphin species is still rare. It has been found that larger groups of orcas have a higher detectability of prey, maximize energy intake per time, and allow for alloparental care, but they are also more likely to be detected by their prey (Baird, 1994; Baird and Dill, 1996). As discussed in Connor (2000), one expects to find similar correlates of group living and size in dolphins as in terrestrial social mammals (mainly carnivores and primates). Intraspecific studies have found that bigger groups use less energy during prey capture (Creel and Creel, 1995), help in the early detection and defense against predators (Caine, 1991; Caldecott et al., 1996; Hoogland, 1981; Isbell and Young, 1993; van Schaik and van Noordwijk, 1986; Waterman, 1997), and help in the defense of territory, females, or feeding resources against conspecifics (McComb et al., 1994; Creel and Creel, 1995; Grinell et al., 1995; Heinsohn and Packer, 1995; Hector, 1986; Packer et al., 1990). However, bigger groups face a higher level of intragroup competition for food (Caldecott et al., 1996; Isbell and Young, 1993), are more obvious to their predators (Boesch, 1991), and need more time for social behavior to maintain cohesion within a group (Henzi et al., 1997).

In interspecific comparisons, similar correlates of group size have been investigated. On one hand, bigger groups minimize variability in hunting success or decrease risk of injury (Packer, 1986), allow for easier access to mates (Andelman, 1986; Gittleman, 1989), facilitate information transfer and social learning (MacDonald, 1983; Gittleman, 1989; Pacala et al., 1996), and exhibit alloparental behavior and defense of young (McComb et al., 1994; MacDonald, 1983; Packer, 1986; Packer et al., 1990; Pusey and Packer, 1994). On the other hand, bigger groups increase competition for food (Andelman, 1986; Gittleman, 1989), use more energy for movement between feeding sites (Clutton-Brock and Harvey, 1977; Creel, 1997), and suffer from more intragroup aggression (Gittleman, 1989).

Here I present the first quantitative intraspecific compari-

sons of group size for eight species of dolphins and porpoises. I searched for the statistical dependence of group size on variables of behavioral ecology reflecting mainly the diet and the predation risk of each species.

METHODS

Species

The phylogeny of the Delphinoidea is not well resolved (LeDuc et al., 1999; Rice, 1998). There are closely related (allopatric) species such as *Tursiops truncatus* and *T. aduncus, Delphinus delphis* and *D. capensis,* and *Globicephala melas* and *G. macrorhynchus* that may share a similar ecology and are accepted as species by some authors but not by others (Bernard and Reilly, 1999; Evans, 1994; Wells and Scott, 1999).

On the other hand, it is known that bottlenose dolphins (Dowling and Brown, 1993), striped dolphins (Garcia-Martinez et al., 1997), and harbor porpoises (Andersen, 1993; Börjesson and Berggren, 1997; Gao and Gaskin, 1996, 1998; Rosel et al., 1995; Wang and Berggren, 1997; Wang et al., 1996) differ morphologically and genetically within small geographic areas (e.g., along the coast of an ocean) and/or differ markedly between oceans, implying the existence of morphologically similar subspecies. Additionally, at least in some regions and some species, such as bottlenose dolphins (Hersh, 1990; Hoelzel et al., 1998), common dolphins (Rosel et al., 1994), and killer whales (e.g., Ford et al., 1994; Morton, 1990), sympatric populations occur that differ genetically and ecologically (forming sympatric ecotypes) but that are considered to belong to the same species nonetheless.

Thus, I opted to view the concept of species in the Delphinoidea rather widely and chose to include more cases per species to be able to perform a reasonable analysis rather than restrict myself to pure species, which seem hard to define in the Delphinoidea. I only included species in the present analysis that had more than 20 entries in a larger data set (see next section). These were the three larger Delphinidae killer whale (*Orcinus orca*), pilot whale (*Globicephala* spp.), and Risso's dolphin (*Grampus griseus*), the three smaller Delphinidae bottlenose dolphin (*Tursiops* spp.), common dolphin (*Delphinus* spp.), and striped dolphin (*Stenella coeruleoalba*), and the two Phocoenidae harbor porpoise (*Phocoena phocoena*) and Dall's porpoise (*Phocoenoides dalli*).

Database

The data for the present study are part of a larger database that has been gathered from published and unpublished literature (Gygax, 2000; see also http://www.proximate-biology.ch/lgygax/phd/info.html for more details on the database and the publications it was based on). The aim of the database was to collect data on group size in Delphinoidea and to complement these data with information on life history, physical environment, and diet. Single studies reporting group size were chosen as the replicates to include as much variability in group sizes as possible but to ensure that only data from one location (''population'') contributed to the reported numbers.

A case in the database was defined by each (independent) study that reported some measure of group size. This information was then complemented. In most cases environmental variables were complemented with the aid of depth and surface temperature maps. Information on the life-history variables came from one or several other publications, as did information on prey. All values are local means (e.g., body length is the average length achieved by animals of a certain species in a certain geographical region). If several sets of information for one species and region were available for group size and diet and/or life-history data, I randomly combined the different kind of information. If no information was available for a given species in a specific region, I chose the information from the geographically closest location as the best estimate. This choice was based on the assumption that animals in geographically close regions are similar and that, in principal, they would have values in these variables that are similar to those of near regions.

Response variable: average group size

Because in most available publications average group size was either reported or could be calculated, I chose average group size as the response variable. Other group size measurements such as the median and also measures of variability in group size were highly correlated to average group size and would have yielded similar results (Gygax, unpublished data).

Explanatory variables

I included a restricted set of variables from the whole database in the present analysis because the number of cases was limited for most species, and the idea was to use the same model for all species to make a comparison easy. Thus, variables that were important in an interspecific context (Gygax, in press) or that were presumed to be more important in an intra- rather than interspecific context were included in the present evaluations.

Life-history parameters

Because only one value per species was available for many life-history variables (especially for those regarding maturation and reproduction), only two such variables were included in the analysis. The residency pattern indicates whether the animals were observed year-round in the location where the study was performed or for only part of the year with an additional indication that the animals moved elsewhere. In some locations animals showed a mixed pattern (some individuals could be observed year-round and others not). Only killer whales and bottlenose dolphins had intraspecific variability in this variable. The second life-history variable is the mean asymptotic body length of females. Only one estimate was available for this variable in Dall's porpoise and could thus not be included in the evaluation for that species.

Physical environment

I considered several characteristics of the physical environment for the analysis. The ''habitat'' is given on an ordered scale from riverine, inshore, coastal, continental shelf, and slope to offshore and was coded with the values 0–5. The ''habitat structure'' is either low (straight coastline, open ocean), moderate (some islands with smooth outlines, convoluted underwater topography on the shelf or shelf slope), or high (convoluted coastline or many islands or islands with convoluted coastlines). This was coded with the values 1, 3, and 5. Values of 2 and 4 were used for intermediate situations.

The ''typical depth'' is the measure of water depth in the area of the observations, and the ''range of depths'' is the maximum minus minimum depth.

The ''latitude'' was coded in degrees from the equator (0°–90° to the north or south). The ''typical temperature'' is the measure of the water temperature in degrees Kelvin during the time and in the area of the observations, and the ''range of temperature'' is the average maximum minus average minimum temperature in the same area.

Some of the variables of the physical environment are highly correlated. Thus, the variables of the physical environment

Table 1
PC loadings for the standardized variables describing the physical environment

	Openness (PC1)	Warmth (PC2)	Specificity (PC3)	Smoothness (PC4)
Explained variance				
Individual	0.46	0.27	0.13	0.06
Cumulative	0.46	0.73	0.86	0.92
Habitat	0.491	0.009	−0.040	0.018
Habitat structure	−0.475	−0.046	0.027	−0.821
Typical depth	0.526	−0.025	0.021	−0.364
Range of depth	0.503	−0.104	−0.062	−0.405
Latitude	−0.014	−0.680	0.176	−0.040
Typical temperature	0.020	0.675	−0.201	−0.164
Range of temperature	−0.062	−0.262	−0.960	0.021

were subjected to a principal components analysis (PCA; Table 1) prior to inclusion in the statistical models. The three first principal components, of which two were also of some importance in an interspecific comparison, are considered here for their linear and quadratic effect (i.e., whether group size shows a correlation with these PCs or whether there is a U- or inverse U-shaped dependence). ''Openness'' increases in its value for more open habitat and deeper water and larger depth ranges and decreases with habitat structure. Thus, the farther offshore (less structured, more open, deeper), the higher the value of this PC. ''Warmth'' increases with temperature and decreases with latitude and is thus a direct reflection of the temperature, and ''specificity'' increases in value with decreasing range of temperature and thus with decreasing variability of temperature and is a measure of the temperature specificity that is reflected in the habitats.

Diet

Three food categories were considered in the present analysis: cephalopods, fishes, and mammals/birds. I did not include the small invertebrates (mainly crustacea) in the analysis because it is often not known whether they are prey of the dolphins or had been eaten by fishes that were later eaten by the dolphins.

In the present analysis only the prey occurrence variables are included because they were available for more cases than the other variables. These are indicator variables that describe the occurrence of the three food categories in the diet, the three food categories split by where in the water column the prey occurs (benthic, mesopelagic, pelagic), and further split by whether prey occurs singly, in groups or both.

Again, some of these diet variables were highly correlated and thus subjected to a PCA prior to inclusion into the evaluation. Here I tested the linear effect of the first six PCs of all prey occurrence variables that explain 94% of the variability (Table 2).

The first of these PCs is a contrast between the fish and cephalopod variables (positive contribution) and the mammal variables (negative contribution); in other words, populations with a lot and diverse fish and cephalopods in their diet and

Table 2
PC loadings for the standardized variables describing the occurrence of different diet items according to their rough ecology: the location in the water column (meso. = mesopelagic) and their occurrence in groups, singly, or both

			PC1	PC2	PC3	PC4	PC5	PC6
Explained variance								
Individual			0.32	0.18	0.14	0.12	0.09	0.09
Cumulative			0.32	0.50	0.64	0.76	0.85	0.94
Cephalopds			0.238	0.200	0.290	−0.010	−0.037	−0.021
Fishes			0.194	−0.295	−0.049	−0.152	0.190	0.003
Mammals			−0.305	−0.182	0.316	−0.020	0.031	−0.110
Cephalopds	Pelagic		0.165	0.179	0.367	−0.194	0.132	0.318
Cephalopds	Meso.		0.181	0.237	0.127	−0.158	−0.320	−0.346
Cephalopds	Benthic		0.187	0.030	0.199	0.449	0.072	−0.149
Fishes	Pelagic		0.168	−0.355	−0.056	−0.185	−0.092	−0.038
Fishes	Meso.		0.244	−0.101	−0.016	−0.071	0.487	−0.141
Fishes	Benthic		0.216	−0.303	0.092	0.061	−0.267	0.097
Mammals	Pelagic		−0.305	−0.182	0.316	−0.020	0.031	−0.110
Cephalopds	Pelagic	Both	0.163	0.174	0.369	−0.199	0.127	0.285
Cephalopds	Pelagic	Groups	0.083	0.147	0.140	0.078	0.045	0.252
Cephalopds	Meso.	Both	0.185	0.213	0.135	−0.128	−0.275	−0.351
Cephalopds	Meso.	Groups	0.072	0.118	0.049	−0.339	−0.139	−0.108
Cephalopds	Benthic	Singly	0.063	0.071	0.103	0.160	0.036	−0.094
Cephalopds	Benthic	Both	0.174	0.054	0.222	0.419	0.051	−0.099
Cephalopds	Benthic	Groups	0.093	−0.012	−0.020	0.248	0.134	−0.439
Fishes	Pelagic	Singly	0.046	−0.038	−0.017	0.064	0.024	0.124
Fishes	Pelagic	Both	0.136	−0.132	0.076	−0.258	0.017	−0.041
Fishes	Pelagic	Groups	0.185	−0.321	−0.033	−0.128	−0.105	−0.068
Fishes	Meso.	Both	0.250	−0.083	−0.039	−0.061	0.459	−0.132
Fishes	Meso.	Groups	0.106	−0.085	0.054	−0.187	0.098	−0.240
Fishes	Benthic	Singly	0.140	−0.149	0.046	0.249	−0.070	0.220
Fishes	Benthic	Both	0.228	−0.275	0.092	0.023	−0.225	0.108
Fishes	Benthic	Groups	0.163	−0.252	0.122	0.193	−0.233	0.135
Mammals	Pelagic	Singly	−0.200	−0.129	0.320	−0.069	0.173	−0.018
Mammals	Pelagic	Both	−0.153	−0.157	0.215	−0.008	−0.103	−0.154
Mammals	Pelagic	Groups	−0.292	−0.180	0.301	−0.014	0.035	−0.110

Combinations that do not appear were not found as prey in the literature.

little mammalian prey have high values in this PC. The second PC is a contrast between the cephalopod variables (positive contribution) and the fish and mammal variables (negative contribution), the third PC has positive contributions from both the cephalopod and mammal variables, the fourth is a contrast between the occurrence of benthic and mesopelagic cephalopods, the fifth is a contrast between mesopelagic fish (positive) and mesopelagic cephalopods (negative contribution), and the sixth is a contrast between epipelagic (positive) and mesopelagic/benthic cephalopods (negative contribution).

Predators

Predation risk is only available indirectly in the variables that describe the size of the animals and the openness of the habitat. The smaller the size and the more open the habitat, the more vulnerable animals seem to be toward predation.

Statistical methods

I used PCA based on the correlation structure to summarize covarying explanatory variables and to reduce the number of explanatory variables. Because there were indications that residual distributions showed some few outliers and long tails, if compared to a normal distribution, I used robust linear methods for all the other evaluations. Robust linear models deal with the same kind of problems as analysis of variance and regression, but their estimates and tests are not influenced by (few) outliers and/or long tails in the distribution of the residuals (Hampel et al., 1986).

The statistical evaluations and figures were done on a SuSE 5.2 Linux system with R Versions 0.63.1 and 0.64.1 (see http://www.r-project.org). For the PCA R-package "multiv" (version 1.0-1, originally coded by F. Murtagh ported to R by Friedrich Leisch) was used, and for the robust regression method rlm in R-package "MASS" (version 6.1-2, originally coded by W. N. Venables and B. D. Ripley ported to R by Brian Ripley) was used. All methods are described and discussed in Venables and Ripley (1997). Robust model comparisons were conducted using methods "lmRobMM" and "anova" in S-PLUS, version 5.0, release 2, for Sun SPARC. In this procedure a Wald test is computed that is the robust analogue to a global analysis of variance test which tests whether all variables together explain significantly more than the intercept/constant alone (Mathsoft, 1998).

Model assumptions were mainly checked using graphical methods. For each analysis a quantile–quantile plot (residuals versus quantiles of a normal distribution to detect deviations from normality of the residuals), a Tukey–Anscombe plot (residuals versus estimated values to detect heteroscedasticity of the residuals), RS plots (residuals plus component effect versus explanatory variables to detect deviating shapes of the dependencies), and residual-interaction plots (residuals versus two explanatory variables to detect unmodeled two-way interactions) were checked.

For each species, average group size was regressed against female length, openness, warmth, specificity, their squares, and against the six PCs of the prey occurrence variables. Average group size and length were log transformed. For bottlenose dolphins and killer whales, the residency pattern was additionally included, and for the Dall's porpoise the length was excluded due to lack of information on intraspecific variability.

The linear forms of the variables have been normalized for the regression estimate; that is, for variable x, $z_i = (x_i - \bar{x})/\mathrm{SD}(x)$ was used as the explanatory variable, where $\bar{x}$ is the mean of variable x and $\mathrm{SD}(x)$ the standard deviation of x. The coefficients were estimated with the following structural part of the model, where gs is the group size, I is the intercept, E_{rp} is the effect of the residency pattern, L is the length, the P_i is a PC of the physical environment, D_i is a PC of the diet, and λ, ρ, and δ are the estimated parameters:

$$\log(gs) = I + E_{rp} + \lambda_1 L + \lambda_2 L^2 + \rho_1 P_1 + \rho_2 P_1^2 + \rho_3 P_2 + \rho_4 P_2^2 + \rho_5 P_3 + \rho_6 P_3^2 + \delta_1 D_1 + \delta_2 D_2 + \delta_3 D_3 + \delta_4 D_4 + \delta_5 D_5 + \delta_6 D_6$$

or on the original scale of group size:

$$gs = e^{I} \cdot e^{E_{rp}} \cdot e^{\lambda_1 L + \lambda_2 L^2} \cdot e^{\rho_1 P_1 + \rho_2 P_1^2} \cdot e^{\rho_3 P_2 + \rho_4 P_2^2} \cdot e^{\rho_5 P_3 + \rho_6 P_3^2} \cdot e^{\delta_1 D_1} \cdot e^{\delta_2 D_2} \cdot e^{\delta_3 D_3} \cdot e^{\delta_4 D_4} \cdot e^{\delta_5 D_5} \cdot e^{\delta_6 D_6}.$$

The sample size for a species was given by the cases for which all the explanatory variables were available and ranged from 22 to 87 (Table 3).

Table 3
ANOVA table comparing the full models with the minimal model (including only a constant) for each species

Species	rdf[a]	df	Wald	p
Common dolphin (dd)	11	14	85.50	$\ll .001$
Striped dolphin (sc)	9	14	1342.40	—[b]
Bottlenose dolphin (tt)	60	16	23.35	.10
Risso's dolphin (gg)	13	14	437.14	$\ll .001$
Pilot whale (gs)	10	14	288.14	$\ll .001$
Killer whale (oo)	58	16	43.65	$< .001$
Harbor porpoise (pp)	7	14	151.56	$\ll .001$
Dall's porpoise (pd)	18	12	16.36	.176

A significant p value indicates that at least some explanatory variables correlate significantly with group size.

[a] Residual degree of freedom.

[b] Final estimate using lmRobMM in S-PLUS has high bias.

RESULTS

Group size can be predicted by different explanatory variables in the eight species that were considered in the present evaluations (Figure 1, Table 4). Features of the dependence of average group size on the explanatory variables that are discussed include the shape of the dependence (Figure 1), the statistical significance of the estimated coefficients (Table 4; the statistical significance for the whole models is given in Table 3), and the biological importance of each variable (Table 4). The biological importance of a variable is measured here by the factor describing the change of group size only if this variable is varied through its observed range. This value is compared with the factor that describes the maximum change in average group size that has been observed. If the former is larger than half of the latter, the variable is considered to be biologically important (Table 4).

Length showed a significant correlation with group size in the common dolphin, the Risso's dolphin, and the pilot whales. Length seems to be of biological importance for the common dolphin, the pilot whale, and the harbor porpoise (Figure 1, Table 4). In the bottlenose dolphin, the Risso's dolphin, and the pilot whale, group size decreased with increasing length but decreased less the larger the size (some quadratic effect). In the harbor porpoise maximum group size is reached at an intermediate length, and in the common dolphin maximum group sizes were observed at minimal and maximal length. No dependency of group size on length was

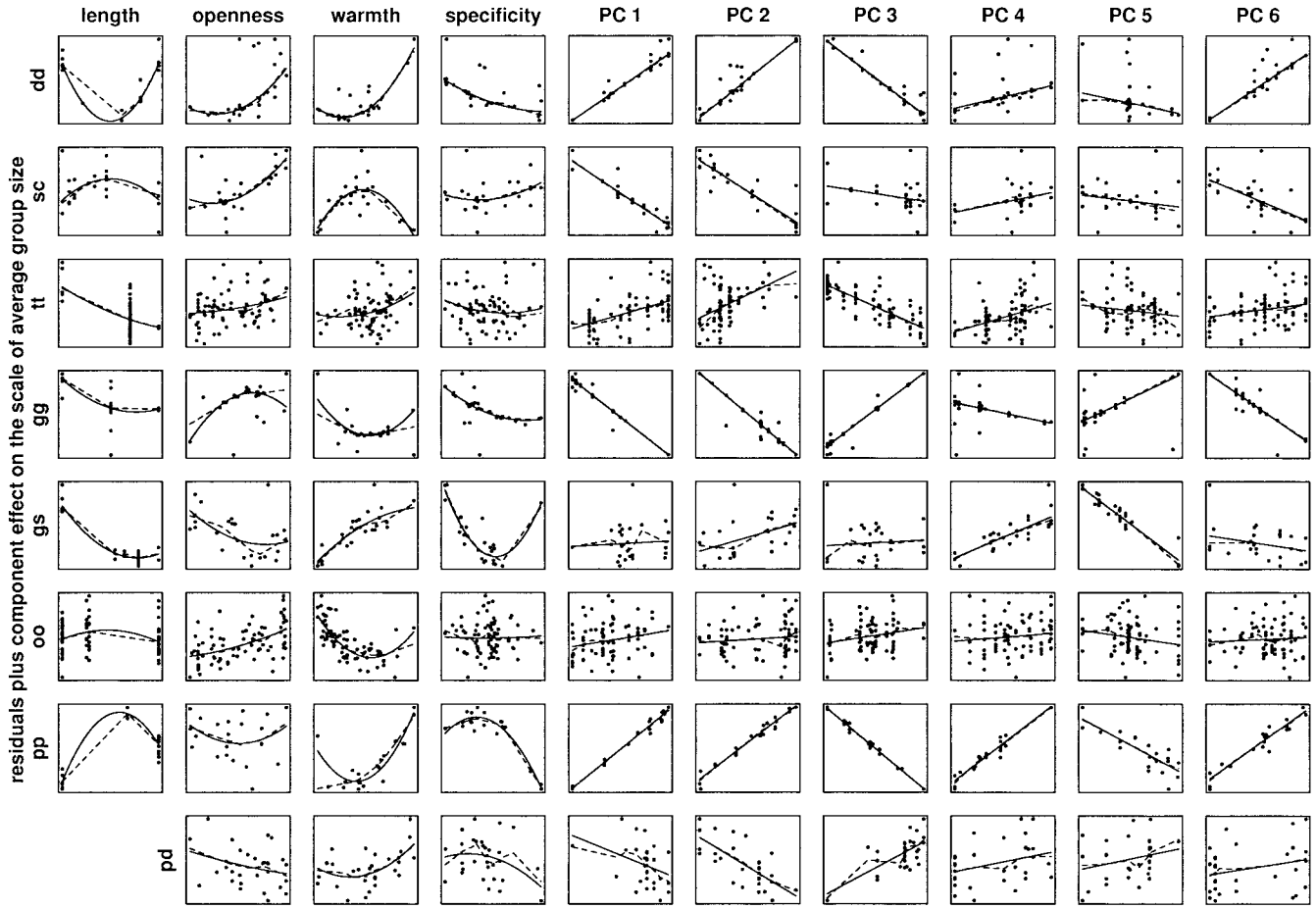

Figure 1
Shapes of dependences of average group size on the explanatory variables. Plotted on the y-axis are the sum of the estimated component effects plus the residuals on a log scale. This is equivalent to the group size if all other explanatory variables are set to zero. Explanatory variables include the length of the females, the three first PCs of the physical environment (openness, warmth, and specificity) and the six PCs of the food occurrence variables (PC1, . . . , PC6). All axes have different scales (though variables are scaled such that they have a standard deviation of one along the x-axis); thus only the shape should be interpreted. The continuous line is the model prediction, and the dashed line the result of a local smoother (loewess). For the biological and statistical significance, see Table 4. For the species, see Table 3.

Table 4
Statistical significance (S) and biological importance (B) of the explanatory variables for explaining group size

	Dolphins												Porpoises			
	Common d.		Striped d.		Bottlenose d.		Risso's d.		Pilot whale		Killer whale		Harbor		Dall's	
	S[a]	B[b]	S	B	S	B	S	B	S	B	S	B	S	B	S	B
Length	*,***	+	†,†	–	‡,†	–	***,**	–	*,†	+	†,†	–	†,†	+		
Openness	‡,†	–	‡,†	–	†,†	–	†,**	–	†,†	–	**,†	–	†,†	–	†,†	–
Warmth	*,*	+	†,‡	–	‡,†	–	†,***	–	*,†	–	***,***	–	‡,‡	–	†,†	–
Specificity	*,†	–	†,†	–	†,†	–	***,**	–	**,**	–	†,†	–	‡,†	++	†,†	–
PC1	**	++	†	–	†	–	***	++	†	–	†	–	†	++	†	–
PC2	*	++	†	–	†	–	***	++	†	–	†	–	‡	++	†	+
PC3	**	++	†	–	†	–	***	++	†	–	†	–	†	++	†	+
PC4	†	–	†	–	*	–	*	–	†	–	†	–	‡	++	†	–
PC5	†	–	†	–	†	–	**	–	†	++	†	–	†	–	†	–
PC6	*	–	†	–	†	–	**	+	†	–	†	–	†	+	†	–

[a] Statistical significance of linear, quadratic term: †$p > .1$; ‡$p < .1$; *$p < .05$; **$p < .01$; ***$p < .001$.

[b] Biological importance: variable on its own can explain (–) less than half the variability in group size; (+) more than half the variability in group size; (++) more than 1 times the variability in group size.

obvious in the striped dolphin and the killer whale (Figure 1, Table 4).

Openness reached significance in Risso's dolphins and killer whales. Group size increases with openness in all species except Dall's porpoise and pilot whales, which showed a decrease in group size with openness, and the harbor porpoise, where no strong relation was apparent (Figure 1, Table 4).

Warmth influenced group size significantly in common dolphins, Risso's dolphins, pilot whales, killer whales, and almost reached significance for bottlenose dolphins and harbor porpoises. It was especially biologically important in common dolphins. Whereas group size increased (quadratically) in common dolphins, pilot whales, and harbor porpoises, it showed a U-shaped relationship in Risso's dolphins and killer whales and an inverted U-shape in striped dolphins. No (strong) dependence was seen in the bottlenose dolphins and the Dall's porpoise (Figure 1, Table 4).

Group size depended significantly on ''specificity'' in common dolphins, Risso's dolphins, and pilot whales and seemed to be of biological importance in harbor porpoises. Group size declined with increasing specificity in common dolphins, Risso's dolphins, and harbor porpoises and showed a U-shape in pilot whales. In the other species group size did not seem to be influenced much by specificity (Figure 1, Table 4).

Average group size also showed some statistically significant and biologically important linear relationships with the PCs of the prey occurrence variables. Again, patterns were diverse from species to species and cannot be described in general terms for all species (Figure 1, Table 4). For example, the common dolphin showed both statistically significant and biologically relevant positive relationships of group size with the first two and a negative relationship with the third PC of the diet variables. The sixth PC again showed a positive significant correlation with group size. No pattern was apparent for the fourth and fifth PC. In the pilot whale only the fifth PC showed a biologically relevant negative correlation with group size, but this did not reach statistical significance.

DISCUSSION

The dependence of group size on ecological parameters was successfully modeled statistically in the current study for common dolphin, striped dolphin, bottlenose dolphin, Risso's dolphin, pilot whale, killer whale, harbor porpoise, and Dall's porpoise.

Costs and benefits: predator avoidance

Starting from the cost–benefit arguments mentioned in the Introduction, there are specific predictions for some of the explanatory variables that were investigated in the current evaluations of group size.

Regarding susceptibility to predators, one would assume that group size correlates negatively with size of the animals and positively with openness of the habitat (the latter could also be shown in an interspecific comparison; Gygax, in press) because small animals and animals in open waters seem more vulnerable to predators. This pattern is apparent in Risso's dolphins and weak in bottlenose dolphins. A negative correlation with size can be seen in pilot whales and a positive correlation with openness in killer whales (but see below) and striped dolphins. Common dolphins do show a positive correlation with openness, but their dependence of group size on length is U-shaped (Figure 1).

Although group size as an antipredator strategy might potentially be a reasonable hypothesis for striped, bottlenose, and Risso's dolphins and pilot and killer whales, this hypothesis cannot be assumed for common dolphins and harbor and Dall's porpoises based on the current data. In harbor porpoises this could be because they follow a cryptic strategy as their antipredator behavior (judged by their coastal habitat; Read, 1999). It is harder to explain this pattern for common dolphins and Dall's porpoises because they typically occur offshore where predation pressure is thought to be highest. It is also surprising that group size for killer whales should follow a pattern of antipredator strategies, as they are a top predator themselves (e.g., Guinet, 1991; Hoelzel, 1993; Lopez and Lopez, 1985; Similä, 1996). This suggests that either openness of habitat is not a good indicator for actual predation pressure or that bigger groups are only one possible antipredator strategy used by these small-toothed whales.

Costs and benefits: diet selection

Group sizes might also differ depending on diet. The explanatory variables of interest here are warmth, specificity, and the PCs of the prey occurrence variables. The variability of group size with warmth and specificity can be described in general as U-shaped. The variability of the exact shape is huge for both warmth and specificity (Figure 1). The PCs of the food occurrence variables show no consistent pattern over the different species. Thus, no general conclusions about the evolution and/or maintenance of group size of these species in dependence on their type and rough ecology of prey can be drawn.

It seems that pilot whales, for example, decrease their group sizes when they feed more on mesopelagic fish and less on mesopelagic cephalopods. Common dolphins increase their group size if they feed on more varying types of fish (and cephalopods, PC1), if they feed more on cephalopods and less on fish (PC2), if they feed on specific cephalopods (PC3), and if they feed more on epipelagic and less on mesopelagic/benthic cephalopods (PC6).

These correlations with food-related variables are difficult to interpret without more detailed knowledge on the behavioral strategies used in capturing prey and on prey distribution and their predator avoidance strategies. Either bigger groups are necessary in Delphinoidea to feed cooperatively on certain type(s) of prey (occurring under certain environmental conditions), or certain types of prey may occur in larger patches and thus enable these mammals to feed bigger groups. However, the opposite may also be true, in that larger groups can coincide with smaller patches. This happens when a group of animals depletes a patch and then, still hungry, moves on to the next patch, which may in turn be depleted (te Boekhorst and Hogeweg, 1994).

Patterns due to unrecognized species

The patterns in bottlenose and common dolphins might originate from the fact that in these two species, (sympatric) coastal and offshore populations differ in morphology and also in group size. Thus we may be looking at ecologically distinct subspecies (Hersh, 1990; Hoelzel et al., 1998; Rosel et al., 1994). It is not clear, however, what the increased group size in these offshore forms is an adaptation for, although there are claims that niches differ according to water temperature, depth, prey diversity, and prey species composition (Hoelzel et al., 1998). Similarly, the pattern for killer whales could possibly be explained by different ecotypes with bigger groups found offshore (e.g., Ford et al., 1994; Mikhalev et al., 1981; Morton, 1990), but too little is known about the behavioral strategies of these animals living far from shore.

If we take the currently used species at face value, we can ask whether the observed patterns reflect the phylogeny of these species. It seems clear that the common dolphin, the

striped dolphin, and the bottlenose dolphin are more closely related to each other than to the other Delphinidae or the Phocoenidae (LeDuc et al., 1999). The two Phocoenidae species should also be more closely related to each other than to the Delphinidae. Thus, if the patterns reflect phylogeny, they should be more similar within these two groups of species than in comparison to the larger Delphinidae, for instance. This does not seem to be the case in general, as no species group seems to have the same dependency of group size on the investigated explanatory variables (Figure 1). The two Phocoenidae do show similar patterns in their variables of the physical environment but less so in their diet. This could easily be explained if the species-specific adaptation has mostly taken place in regard to the diet and less so in regard to the possibly more stable physical environment. This notion is not to be generalized, though, as the three Delphininae do not even show a consistent pattern in the dependence of their group size on the variables of the physical environment.

General conclusions

It is striking that species either show dependence of group size on many variables at the same time or on almost no variable at all (Table 4), but it remains unclear why. At most, there is a story for each of the species. This is not further pursued here, as these are likely to be post-hoc just-so stories. In other words, knowing the outcome of the evolutionary process, one can always find reasons why this specific evolutionary pathway has been selected for and not another. But without substantial evidence, these are nothing more than tales and may as well be due to a random historical process as to different selective pressures acting on the different species.

On the whole, it is obvious that group size seems to depend on different sets of variables in each species. It is not surprising, then, that I found species to be the most important variable in an interspecific comparison of group sizes in the Delphinoidea (Gygax, in press). Unfortunately, it is still possible that the data available for the current study are too scanty. Patterns may change if detailed knowledge of these species becomes available and proper populations can be used as replicates in an analysis.

Plasticity in social systems is hypothesized to co-occur with niche breadth (Lott, 1984). This might result in all Delphinoidea species having a similar predisposition in kind and variety of social systems because, in general, it seems difficult to defend resources and space is vast at the surface of oceans, and thus niches might be wide for all the Delphinoidea species.

It seems important to know more about the proximate behavior (e.g., feeding or predator avoidance strategies) to interpret its function and possible origin and/or to see how simple behavioral rules might lead to an observed pattern without the necessity of a complex cost–benefit analysis. The latter is often supported by dynamic individual based modeling (Hemelrijk, 1996, 1997), which can help form hypotheses on proximate mechanism that can, in turn, be tested in the wild.

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REFERENCES

Andelman SJ, 1986. Ecological and social determinants of cercopithecine mating patterns. In: Ecological aspects of social evolution: birds and mammals (Rubenstein DI, Wrangham RW, eds). Princeton, New Jersey: Princeton University Press; 201–216.

Andersen LW, 1993. The population structure of the harbour porpoise *Phocoena phocoena* in Danish waters and part of the North Atlantic. Mar Biol 116:1–7.

Baird RW, 1994. Foraging behaviour and ecology of transient killer whales (*Orcinus orca*) (PhD dissertation). Vancouver: Simon Fraser University.

Baird RW, Dill LM, 1996. Ecological and social determinants of group size in transient killer whales. Behav Ecol 7:408–416.

Bernard H, Reilly SB, 1999. Pilot whales *Globicephala* (Lesson, 1828). In: Handbook of marine mammals, vol. 6. The second book of dolphins and the porpoises (Ridgway SH, Harrison RJ, eds). San Diego, California: Academic Press; 245–279.

Boesch C, 1991. The effect of leopard predation on grouping patterns in forest chimpanzees. Behaviour 117:220–242.

Börjesson P, Berggren P, 1997. Morphometric comparisons of the skulls of harbour porpoises (*Phocoena phocoena*) from the Baltic, Kattegat, and Skagerrak seas. Can J Zool 75:280–287.

Caine NG, 1991. Flexibility and cooperation as unifying themes in *Sanguinus* social organization and behavior: the role of predation pressures. In: Marmosets and tamarins: systematics, ecology and behaviour (Rylands A, ed). Oxford: Oxford University Press; 200–219.

Caldecott JO, Feistner ATC, Gadsby EL, 1996. A comparison of ecological strategies of pigtailed macaques, mandrills and drills. In: Evolution and ecology of macaque societies (Fa JE, Lindburg DG, eds). Cambridge: Cambridge University Press; 73–94.

Clutton-Brock TH, Harvey PH, 1977. Primate ecology and social organisation. J Zool 183:1–39.

Connor RC, 2000. Group living in whales and dolphins. In: Cetacean societies (Mann J, Connor RC, Tyack P, Whitehead H, eds). Chicago: University of Chicago Press; 199–218.

Creel S, 1997. Cooperative hunting and group size: assumptions and currencies. Anim Behav 54:1319–1324.

Creel S, Creel NM, 1995. Communal hunting and pack size in African wild dogs, *Lycaon pictus*. Anim Behav 50:1325–1339.

Dowling TE, Brown WM, 1993. Population structure of the bottlenose dolphin *Tursiops truncatus* as determined by restriction endonuclease analysis of mitochondrial DNA. Mar Mammal Sci 9:138–155.

Evans WE, 1994. Common dolphin, white-bellied porpoise—*Delphinus delphis* Linnaeus, 1758. In: Handbook of marine mammals, vol. 5. The first book of dolphins (Ridgway SH, Harrison RJ, eds). London: Academic Press; 191–224.

Ford JKB, Ellis GM, Balcomb KC, 1994. Killer whales. Vancouver: University of British Columbia Press.

Gao A, Gaskin DE, 1996. Geographical variation in metric skull characters among proposed subpopulations and stocks of harbor porpoise, *Phocoena phocoena,* in the Western North Atlantic. Mar Mammal Sci 12:516–527.

Gao A, Gaskin DE, 1998. Geographical variation of the harbour porpoise, *Phocoena phocoena,* evaluated by discriminant analysis. Mar Mammal Sci 14:649–652.

Garcia-Martinez J, Raga JA, Latorre A, 1997. Population structure of striped dolphins (*Stenella coeruleoalba*) in European waters based on mitochondrial DNA. In: Proceedings of the Tenth Annual Conference of the European Cetacean Society, Lisbon, Portugal (Evans PGH, ed). Kiel, Germany: European Cetacean Society; 303.

Gittleman J, 1989. Carnivore group living: comparative trends. In: Carnivore behavior, ecology and evolution (Gittleman J, ed). Ithaca, New York: Cornell University Press; 183–207.

Gittleman JL, Decker DM, 1994. The phylogeny of behaviour. In: Behaviour and evolution (Slater PJB, Halliday TR, eds). Cambridge: Cambridge University Press; 80–105.

Grinell J, Packer C, Pusey AE, 1995. Cooperation in male lions: kinship, reciprocity or mutualism. Anim Behav 49:95–105.

Guinet C, 1991. Intentional stranding apprenticeship and social play in killer whales (*Orcinus orca*). Can J Zool 69:2712–2716.

Gygax L, 2000. Group size and behavioural ecology in Delphinoidea (PhD dissertation). Zürich: University of Zürich.

Gygax L, in press. Evolution of group size in the superfamily Delphin-

oidea (Delphinidae, Phocoenidae and Monodontidae): a quantitative comparative analysis. Mammal Rev.
Hampel FR, Ronchetti EM, Rousseeuw PJ, Stahel WA, 1986. Robust statistics: the approach based on influence functions. New York: John Wiley & Sons.
Hector DP, 1986. Cooperative hunting and its relationship to foraging success and prey size in an avian predator. Ethology 73:247–257.
Heinsohn R, Packer C, 1995. Complex cooperative strategies in group–territorial African lions. Science 269:1260–1262.
Hemelrijk C, 1996. Reciprocation in apes: from complex cognition to self-structuring. In: Great ape societies (McGrew WC, Marchant LF, Nishida T, eds). Cambridge: Cambridge University Press; 185–195.
Hemelrijk CK, 1997. Cooperation without genes, games or cognition. In: Proceedings of the Fourth European Conference on Artificial Life, ECAL97 (Husbands P, Harvey I, eds). Cambridge: MIT Press/Bradford Books; 511–520.
Henzi SP, Lycett JE, Weingrill T, 1997. Cohort size and the allocation of social effort by female mountain baboons. Anim Behav 54:1235–1243.
Hersh SL, 1990. Distinction between northwest Atlantic offshore and coastal bottlenose dolphins based on hemoglobin profile and morphometry. In: The bottlenose dolphin (Leatherwood S, Reeves RR, eds). San Diego, California: Academic Press; 129–139.
Hoelzel AR, 1993. Foraging behaviour and social group dynamics in Puget Sound killer whales. Anim Behav 45:581–891.
Hoelzel AR, Potter CW, Best PB, 1998. Genetic differentiation between parapatric 'nearshore' and 'offshore' populations of the bottlenose dolphin. Proc R Soc B 265:1177–1183.
Hoogland JL, 1981. The evolution of coloniality in white-tailed and black-tailed prairie dogs (Sciuridae: *Cenomys leucrus* and *C. ludocianus*). Ecology 62:252–272.
Isbell LA, Young TP, 1993. Social and ecological influences on activity budgets of vervet monkeys, and their implication for group living. Behav Ecol Sociobiol 32:377–385.
LeDuc RG, Perrin WF, Dizon AE, 1999. Phylogenetic relationships among the Delphinid cetaceans based on full cytochrome *B* sequences. Mar Mammal Sci 15:619–648.
Lee PC, 1994. Social structure and evolution. In: Behaviour and evolution (Slater PJB, Halliday TR, eds). Cambridge: Cambridge University Press; 266–303.
Lopez JC, Lopez D, 1985. Killer whales (*Orcinus orca*) of Patagonia, and their behaviour of intentional stranding while hunting nearshore. J Mammal 66:181–183.
Lott DF, 1984. Intraspecific variation in the social systems of wild vertebrates. Behaviour 88:266–325.
MacDonald DW, 1983. The ecology of carnivore social behaviour. Nature 301:379–384.
Mathsoft, 1998. Robust regression. In: S-PLUS 5—Guide to statistics. Seattle, Washington: Data Analysis Products Division, Mathsoft; 209–246.
McComb K, Packer C, Pusey A, 1994. Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*. Anim Behav 47:379–387.
Mikhalev YA, Ivashin MV, Savusin VP, Zelenaya FE, 1981. The distribution and biology of killer whales in the southern hemisphere. Rep Int Whal Comm 31:551–566.
Morton AB, 1990. A quantitative comparison of the behaviour of resident and transient forms of the killer whale off the central British Columbia coast. In: Individual recognition of cetaceans: use of photo-identification and other techniques to estimate population parameters (Hammond PS, Mizroch SA, Donovan GP, eds). Cambridge: International Whaling Commission; 245–248.
Pacala SW, Gordon DM, Godfray HCJ, 1996. Effects of social group size on information transfer and task allocation. Evol Ecol 10:127–165.
Packer C, 1986. The ecology of sociality in felids. In: Ecological aspects of social evolution: birds and mammals (Rubenstein DI, Wrangham RW, eds). Princeton, New Jersey: Princeton University Press; 429–451.
Packer C, Scheel D, Pusey AE, 1990. Why lions form groups: food is not enough. Am Nat 136:1–19.
Pusey AE, Packer C, 1994. Non-offspring nursing in social carnivores: minimizing the costs. Behav Ecol 5:362–374.
Read AJ, 1999. Harbour porpoise *Phocoena phocoena* (Linnaeus, 1758). In: Handbook of marine mammals, vol. 6. The second book of dolphins and the porpoises (Ridgway SH, Harrison RJ, eds). San Diego, California: Academic Press; 323–355.
Rice DW, 1998. Marine mammals of the world; systematics and distribution. Lawrence, Kansas: Society of Marine Mammalogy.
Rodman PS, 1988. Resources and group sizes of primates. In: The ecology of social behaviour (Slobodchikoff CN, ed). San Diego, California: Academic Press; 83–108.
Rosel PE, Dizon AE, Haygood MG, 1995. Variability of the mitochondrial control region in populations of the harbour porpoise, *Phocoena phocoena,* on interoceanic and regional scales. Can J Fish Aquat Sci 52:1210–1219.
Rosel PE, Dizon AE, Heyning JE, 1994. Genetic analysis of sympatric morphotypes of common dolphins (genus Delphinus). Mar Biol 119:159–167.
Similä T, 1996. Occurrence and diet of killer whales in northern Norway: seasonal patterns relative to the distribution and abundance of Norwegian spring-spawning herring. Can J Fish Aquat Sci 53: 769–779.
te Boekhorst IJA, Hogeweg P, 1994. Effects of tree size on travelband formation in orang-utans: data analysis suggested by a model study. In: Artificial life IV (Brooks RR, Maes P, eds). Cambridge: MIT Press; 119–129.
Terborgh J, Janson CH, 1986. The socioecology of primate groups. Annu Rev Ecol Syst 17:111–135.
van Schaik CP, van Hoof JARAM, 1983. On the ultimate causes of primate social systems. Behaviour 85:91–117.
van Schaik CP, van Noordwijk MA, 1986. The evolutionary effect of the absence of felids on the social organization of the Simeulue monkey (*Macaca fascicularis Fusca*). Folia Primat 44:138–147.
Venables WN, Ripley BD, 1997. Modern applied statistics with S-PLUS. New York: Springer.
Wang JY, Berggren P, 1997. Mitochondrial DNA analysis of harbour porpoise (*Phocoena phocoena*) in the Baltic Sea, the Kattegat–Skagerrak seas and off the west coast of Norway. Mar Biol 127:531–537.
Wang JY, Gaskin DE, White BN, 1996. Mitochondrial DNA analysis of harbour porpoise, *Phocoena phocoena,* subpopulations in North American waters. Can J Fish Aquat Sci 53:1632–1645.
Waterman JM, 1997. Why do male Cape ground squirrels live in groups? Anim Behav 53:809–817.
Wells RS, Scott MD, 1999. Bottlenose dolphin *Tursiops truncatus* (Montagu, 1821). In: Handbook of marine mammals, vol. 6. The second book of dolphins and the porpoises (Ridgway SH, Harrison RJ, eds). San Diego, California: Academic Press; 137–182.
Wrangham RW, 1980. An ecological model of female-bonded primate groups. Behaviour 75:262–300.